

# Drought sensitivity and stem growth variation of nine alien and native tree species on a productive forest site in Germany

Nils Hoffmann<sup>a,\*</sup>, Peter Schall<sup>a</sup>, Christian Ammer<sup>a</sup>, Bertram Leder<sup>b</sup>, Torsten Vor<sup>a</sup>

<sup>a</sup> Department of Silviculture and Forest Ecology of the Temperate Zones, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Büsgenweg 1, D-37077 Göttingen, Germany

<sup>b</sup> Centre of Silviculture and Forest Propagation Consulting, Training and Test Forestry Office Arnsberg, State Forestry and Wood Commission of Nordrhein-Westfalen, Obereimer 2a, D-59821 Arnsberg, Germany

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## ABSTRACT

Many non-native tree species have been introduced to Europe to improve forest productivity. It is assumed that some of these species are better able than native species to mitigate negative effects of climate change. A high growth-related tolerance to climatic extremes is essential to qualify a tree species' suitability for cultivation and must be quantified before initiating adaptation measures. This study investigated basal area and volume increment (BAI and VI) data at various stem height positions to evaluate inter-annual growth variation (mean sensitivity) and drought tolerance of seven alien tree species (*Acer rubrum* L., *Betula maximowicziana* Regel, *Castanea sativa* Mill., *Cryptomeria japonica* D. Don, *Metasequoia glyptostroboides* Hu et Cheng, *Thuja plicata* Donn and *Tsuga heterophylla* Sarg.) which are considered stress tolerant, and two native species (*Fagus sylvatica* L., *Picea abies* H. Karst.) in the Arboretum Burgholz in West Germany. We found that mean sensitivity and response to drought (*resistance*, *recovery*, *resilience*) were related; i.e., sensitive species exhibited greater drought response than less sensitive species. In the drought years 2003, 2006 and 2010/2011, VI of the highly sensitive species *C. japonica* and *P. abies* and rather moderate sensitive *A. rubrum* decreased most strongly (36%), while less sensitive *C. sativa* and *T. heterophylla* were the most resistant tree species (25% decrease). *B. maximowicziana*, *F. sylvatica*, *M. glyptostroboides* and *T. plicata* were moderately sensitive to drought events (growth depression by 29%). *Recovery* after drought showed mainly a reverse response pattern; species with lower *resistance* recovered faster, but this trade-off was not uniform among species. Across drought events, we observed high variation in the response of individual trees and between different tree species. This finding indicates that species' drought sensitivity depends strongly on the drought's onset, duration and frequency. Along tree stems, mean sensitivity and response to drought in 2003 decreased species-specifically from lower to upper stem section height. Thus, quantifying drought sensitivity based solely on breast height measures may result in biased estimates of production declines.

## 1. Introduction

Increases in temperature and climate variability (IPCC, 2013) are associated with increases in the future frequency, magnitude and duration of extreme weather events in Europe (Beniston et al., 2007; Smith, 2011). These climatic extremes, i.e. storms, heat waves and severe drought periods (Dai, 2011) have become important drivers of long-term forest ecosystem dynamics (Bréda et al., 2006; Pretzsch et al., 2013). They may modify pathogen and pest regimes and increase the vulnerability of trees to altered site conditions (Bolte et al., 2009). Declines in forest productivity (Ciais et al., 2005) and higher tree mortality (Allen et al., 2010; Carnicer et al., 2011) entail hazards to

cultivation of a number of economically relevant native tree species. As a result, adaptive forest management may be obliged to consider exotic tree species and the establishment of mixed forests to reduce risk (Jandl et al., 2015; Neuner et al., 2015). In this context, exotic tree species that seem to be adapted to the expected environmental conditions due to their wide natural and climatological ranges are of special importance (Bolte et al., 2009; Kölling et al., 2009). Properties such as drought tolerance or adaptability to extreme weather conditions in general are of special interest (Choat et al., 2012; Niinemets and Valladares, 2006).

To counteract climatic stress, tree species have developed various anatomical and physiological strategies (George et al., 2015); for example, leaf area control (Le Dantec et al., 2000), stomatal regulation of

\* Corresponding author.

E-mail address: [nils.hoffmann@forst.uni-goettingen.de](mailto:nils.hoffmann@forst.uni-goettingen.de) (N. Hoffmann).

transpiration (McDowell et al., 2008), or biomass allocation to below-ground plant compartments (Delucia et al., 2000; Schall et al., 2012). A tree's drought sensitivity depends in particular on the limitations of its vascular wooden tissue's hydraulic architecture (xylem; Tyree and Ewers, 1991). Cavitation-induced emboli inhibit xylem conductivity and reduce water transport potentials from lower parts of the tree to the sites of photosynthesis (Choat et al., 2012). While direct assessment of embolism resistance is challenging (George et al., 2015), tree growth performance, typically captured by retrospective tree ring analyses, can be used as an indicator of drought susceptibility with less effort. Annual ring formation is coupled with tree water availability and carbon allocation for cambial activity (Hinckley et al., 1979; Zweifel et al., 2006). The growth response to climatic stress conditions can be assessed by tolerance components such as *resistance* ( $R_s$ ), *recovery* ( $R_c$ ), and *resilience* ( $R_l$ ) according to Lloret et al. (2011). These attributes quantify changes in growth patterns during and after climatic disturbances and indicate the capacity of a tree (i) to withstand disturbances, (ii) to recover after drought, and (iii) to regain pre-disturbance growth performance (Lloret et al., 2011). *Resistance*, *resilience*, and *recovery* of major European tree species have been investigated in numerous studies (e.g. George et al., 2015; Knutzen et al., 2017; Zang et al., 2011, 2014). Further investigations have dealt with the effects of tree age and size (Lloret et al., 2011; Zang et al., 2012), competition status and species composition (Carnwath et al., 2016; Merlin et al., 2015; Metz et al., 2016; Pretzsch et al., 2013), thinning and changes in stand density (e.g. Kohler et al., 2010; Sohn et al., 2013) and interactions of growth responses with site, tree, and stand characteristics (Rais et al., 2014; for an overview see Ammer, 2017). However, to date few investigations have taken into account the drought sensitivity of alternative, alien tree species (Eilmann and Rigling, 2012) that are potentially well adapted to changing climate conditions.

Growth measurements at breast height (diameter = DBH and basal area = BA) are conventionally applied in forest research as useful predictors for approximation of tree dimension, biomass production and stand density. Several allometric models use DBH as the key variable to predict tree volume, stem form or diameter at an arbitrary stem location (Kublin et al., 2013). The majority of dendrochronological studies have been based on increment core sampling at breast height (Chhin et al., 2010), taking advantage of relatively long time series (Schweingruber et al., 1990). The underlying assumption is that increment measurements at breast height do not bias whole stem growth patterns or responses to external factors (Latte et al., 2016; Sohn et al., 2012). Hence, growth measures at breast height or stem base (Chhin and Wang, 2005) and volume increment (Corona et al., 1995; Hogg et al., 2005) have shown comparable climate-growth relationships. However, increment changes in upper stem sections were found to be less sensitive to drought (for trees of lower altitude; < 430 m a.s.l.) when compared with diameter increment at breast height (Bouriaud et al., 2005; van der Maaten-Theunissen and Bouriaud, 2012). Increasing climate sensitivity with tree height (Kerhoulas and Kane, 2012; Latte et al., 2016), higher growth recovery for topmost heights after drought stress (Sohn et al., 2012), and inconsistencies in the responses of lower and upper stem segments to temperature and climate moisture have been reported (Chhin et al., 2010). Due to allometric discrepancies, model-based growth projections acquired by breast height measures (e.g. Bauwe et al., 2016; Fernandez-de-Una et al., 2015; Williams et al., 2012) may therefore over- or under-estimate drought tolerance. Validation of height- and volume-related growth responses is needed to better assess tree species' suitability in terms of climatic stress tolerance and productivity.

Here we analysed the growth sensitivity of two native tree species and seven alien tree species introduced to Europe, and the growth response of trees to drought at various tree heights in order to capture intra-tree variability. The aims of this study were to (1) quantify and characterize tree species-specific inter-annual growth variability, to (2) determine *resistance* during, and *recovery* and *resilience* after heat and

drought, and to (3) examine species-specific growth variation at various stem height positions.

## 2. Material and methods

### 2.1. Species selection and study site

The following tree species not native to Europe were selected: *Acer rubrum* L., *Betula maximowicziana* REGEL, *Castanea sativa* MILL., *Cryptomeria japonica* D. DON, *Metasequoia glyptostroboides* HU ET CHENG, *Thuja plicata* DONN and *Tsuga heterophylla* (RAF.) SARG. Besides economic criteria (high growth rates, low management risks), all referred species are characterized by a wide range of climatic amplitudes (e.g. Burns and Honkala, 1990; Praciak, 2013; Roloff et al., 2011; SRC NRW, 1986; Walters and Yawney, 1990). Two of the economically most important European native tree species (*Fagus sylvatica* L. and *Picea abies* H. KARST.), one representing a deciduous and the other a coniferous tree species, were included as reference species. In the following, species will be denoted by genus only (for example *Thuja plicata* = *Thuja*).

In order to evaluate species growth performance under comparable site conditions, a uniform forest district was chosen. Stands of the tree species mentioned above are located in the Arboretum Burgholz near Wuppertal in North Rhine-Westphalia (West Germany). This Arboretum is characterized by a podzolic Cambisol with poor to moderate nutrient supply, a silty loam soil texture, good soil water supply and a mor humus layer (Wald und Holz NRW, 2013). In addition to similar soil and climatic conditions, all stands were evenly aged (34–58 years) and had undergone the same silvicultural treatment (thinning from above). However, some of the stands were mixed (but dominated by the target species and selected since no alternative monocultures for these rare species exist nearby exist) while others were monospecific (see Table A.1 for details). For the period 1960–2014, annual temperature was 9.8 °C and annual total precipitation sum was 1131 mm. The values for the vegetation period (May–September) were 15.5 °C with 468 mm (DWD, 2015).

### 2.2. Tree sampling, preparation and analysis of stem disks

Six to ten vital and dominant or co-dominant (according to Kraft, 1984) individuals per tree species were selected for stem analysis. Cross-sectional disks were cut along the main stem of the felled target trees at 0.5 m, 1.3 m and subsequently every 2 m to the top (29.3 m for the highest trees, Fig. 1). The dried stem disks were planed, polished with progressively fine grit sandpaper, and scanned at 1200 dpi resolution (A3 scanner 2400 S, Mustek). To minimize eccentric growth effects, tree ring width was measured along four radii at the main cardinal direction using the semiautomatic image analysis software LignoVision™ (version 1.38e, Rinntech e. K., Heidelberg, Germany) with a precision of 0.01 mm (Rinn, 2006). The obtained radial series were post-edited using the TSAP software (TSAP-Win professional version 4.68e Rinntech e. K., Heidelberg, Germany) to verify the synchronicity within each tree and species. After visual crossdating according to the list method (Yamaguchi, 1991) the series were statistically crossdated in a stepwise procedure using averaged reference series according to the “leave-one-out principle” (Bunn, 2010). In the first step we examined the radial series within a stem disk (comparison of radial directions). We then tested the synchronicity within a tree (comparison of height sections). Finally, we checked the simultaneity among the trees using the mean series at 1.3 m stem height (comparison of individuals). The synchronicities were verified using the statistical parameters *Gleichläufigkeit* (Eckstein and Bauch, 1969), *Gleichläufigkeit*-Significance (Rinn, 2005) and *t*-value (Baillie and Pilcher, 1973). A total of 75 trees and 903 stem disks met these criteria and were included in further analyses (Table A.2).

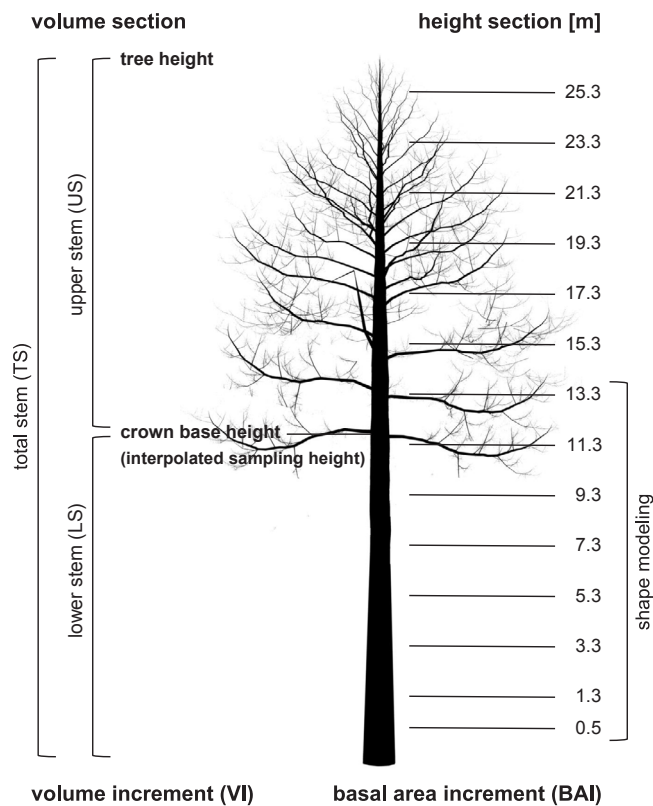


Fig. 1. Schematic illustration of volume and basal area increment height sections; partially adopted and adjusted from Latte et al. (2016). In order to determine the effect of stem height to climate mean sensitivity, resistance, recovery and resilience, response shapes were modelled for the lower eight BAI sections for the common period with corresponding time series length (1998–2012).

### 2.3. Computation of basal area and volume increment (stem analysis)

Annual radial increment (RI) was converted into basal area increment (BAI, for each height section  $BAI_{0.5}$ ,  $BAI_{1.3}$  to  $BAI_{29.3}$ ) since this variable is more representative of whole stem growth when compared with linear measurements (Biondi and Qeadan, 2008; Kohler et al., 2010; Weber et al., 2013). The computation of annual volume increment (VI) was provided by the package *treeglia* using the function *StemAnalysis* (Bascietto and Scarascia-Mugnozza, 2004) of the software R (version 3.2.3, R Core Team 2016). The application uses Carmean's algorithm (Carmean, 1972) to interpolate annual stem heights by estimating inter-annual height increments between examined cross-sections. Under a number of height interpolation methods, Carmean's approach was determined to be the most appropriate with respect to accuracy (e.g. Dyer and Bailey, 1987; Machado et al., 2010). *StemAnalysis* calculates annual volume increments according to Smalian's formula for the computation of a trapezium's volume for the lower stem portions (calculated as sums) and the cone formula for the terminal section's volume (Bascietto and Scarascia-Mugnozza, 2004).

To distinguish between below- and above-crown increments, we linearly interpolated tree ring counts and radial increments (interpolated sampling height) at the measured crown base height ( $H_{CB}$ , height at the lowest green branch of deciduous and the lowest fork with three green branches of coniferous trees). Finally, by application of *StemAnalysis*, volume increments of the following three stem sections were computed: total aboveground stem volume ( $VI_{TS}$ ), volume of the stem section below  $H_{CB}$  ( $VI_{LS}$ ), and volume of the upper stem section above  $H_{CB}$  ( $VI_{US}$ ; Fig. 1). In order to reduce effects of eccentricity, fluting and ovality, species-specific mean series were derived arithmetically from individual height (BAI) and volume (VI) section series.

### 2.4. Chronologies and period selection

For each height and volume section we calculated BAI and VI site chronologies as arithmetic means of the raw series using the R package *dplR* (Bunn, 2008). To account for naturally occurring long- and medium-term variations such as age or diameter related trends (Cook et al., 1990; Fritts, 1976), all series were fitted by a cubic smoothing spline with 50% frequency cutoff at 67% of the series length (e.g. Zang et al. 2012; Metz et al., 2016; Land et al., 2017). The detrending procedure preserves high-frequency variability (climate induced signals) within the series resulting in a dimensionless growth index (I) by calculating the ratio of the raw and predicted increment values (Cook et al., 1990). We used autoregressive modelling of the standardized series to remove first order autocorrelation, expressed as the relationship between the current and previous year values, using the Akaike's Information Criterion (AIC). The resulting residual series from each sample category were averaged to chronologies using a robust biweight mean that reduced effects of outliers relative to their position (Bunn, 2008; Zang et al., 2011).

The common growth period from 1998–2012 was selected for subsequent statistical analysis. For this period, a total of 8 height sections, except for *Metasequoia* (7 sections only), and all three volume sectional chronologies were available for each tree species.

For the description of the overall chronology quality we calculated the effective chronology signal (*es*) and the expressed population signal (*eps*, Wigley et al., 1984) for the common period using *dplR* (Bunn, 2008). *es* is an estimator used to quantify the signal strength for a common chronology signal between trees while *eps* determines how well a finite sample of series data represents the hypothetical population chronology (Buras 2017). To be able to compare data information with former studies, a threshold of *eps* > 0.85 was considered as an acceptable level for a hypothetical noise-free chronology quality (e.g. Brice et al., 2013; Land et al., 2017; Waldboth and Oberhuber, 2009). Additionally, the mean sensitivity (*ms*) was computed for mean series and chronologies to characterize growth dependency from external environmental factors and to evaluate inter-annual variability within the chronologies (Fritts, 1976; Metz et al., 2016). Finally, we calculated Pearson's correlation coefficients for chronologies to estimate relationships between BAI and VI at different height sections.

### 2.5. Climate data and identification of stress events

All climate data (mean and maximum temperature and precipitation sum), which included daily and monthly data for the lifespan of our target trees (1960–2014), were taken from the weather station "Wuppertal-Buchenhofen" (ID 5717, 51° 13.488'N, 7° 6.318'E, 130 m a.s.l.) of the German National Meteorological Service "Deutscher Wetterdienst" (DWD, 2015). The station is located in the centre of the Arboretum with a horizontal distance of 2.3 km to the furthestmost stand (*Castanea*, cf. 403 K1). To identify heat-related drought events in the period 1960–2014, three meteorological variables were considered with respect to divergences from the long-term average during the growing season (May–September): vapour pressure deficit (*vpd*), degree day sums ( $sum_{\Delta t20}$ ), and the standardized precipitation evapotranspiration index (*spei*). Based on the formula of Magnus (Junzeng et al., 2012; Equation A.1), *vpd* was calculated as the difference between saturation- and actual-vapour pressure (Equation A.2). It is an important measure for evaluating transpiration processes and stomatal conductance in plants (Junzeng et al., 2012). The  $sum_{\Delta t20}$  (in °C), which should reflect hot periods, was calculated as the sum of the differences between daily mean temperatures > 20 °C and 20 °C. For *vpd* and  $sum_{\Delta t20}$ , values above 95th percentile were defined as stress events. The novel drought index *spei* was used to identify deficits in precipitation taking into account the effect of temperature on drought development through a basic water balance calculation (Vicente-Serrano et al., 2010). It is an extension of the standardized precipitation index (*spi*,



McKee et al., 1993) and can be determined for varying time scales (moving averaging windows) over previous months. Hence, *spei* allows the identification of and differentiation between long- and short-term drought occurrence for a given climatic time series. It is based on the accumulated water deficit or surplus (water balance), calculated by the difference of the monthly precipitation sum and monthly potential evapotranspiration. In order to identify short- and medium-term drought-intensities with physiological importance for water-shortage in trees and a high probability of occurrence in Central Europe (George et al., 2015), we used one- and three-month intervals. As recommended by McKee et al. (1993), drought severity was classified into categories by the *spei* value as: moderate drought (-1.00 to -1.50), severe drought (-1.50 to -1.99) and extreme drought ( $\leq -2.00$ ). The potential evapotranspiration according to Thornthwaite (1948) and *spei* were calculated with the R package *SPEI* (Beguería and Vicente-Serrano, 2013) based on monthly mean temperature and monthly precipitation sums.

## 2.6. Response indices

Resistance (*Rs*), recovery (*Rc*) and resilience (*Rl*), were calculated to quantify species' growth responses to identified drought events (Lloret et al., 2011). Resistance determines the intensity of growth depression during the corresponding stress year (DY) in relation to the period before drought (preDY). It characterizes the ability of the tree to revoke the stress situation. Recovery reflects the extent of growth increase, or, if  $Rc < 1$ , persistent decrease after the drought event (postDY) and is calculated as the ratio:  $Rc = \text{postDY}/\text{DY}$ . Resilience is defined as the ratio between postDY/preDY. A resilience of 1 indicates the ability of a tree to reach a pre-drought growth level. In order to adequately represent a species growth level before and after stress, and to avoid any interference of previous and/or subsequent DYs, we chose a consistent pre- and post-drought period of 2 years (e.g. Knutzen et al., 2017). The response indices were calculated as the ratios of the detrended increment mean series (growth index *I* of  $BAI_{0.5}$  to  $BAI_{13.3}$  and  $VI_{TS}$ ,  $VI_{LS}$ ,  $VI_{US}$ ) since raw data are usually strongly affected by natural age-related growth trends and variations in tree dimension (Fekedulegn et al., 2003; Kohler et al., 2010; Lloret et al., 2011; Metz et al., 2016; Sohn et al., 2012).

$$Rs = \frac{I_{DY}}{\text{mean}_{I_{2 \text{ pre DY}}}}$$

$$Rc = \frac{\text{mean}_{I_{2 \text{ post DY}}}}{I_{DY}}$$

$$Rl = \frac{\text{mean}_{I_{2 \text{ post DY}}}}{\text{mean}_{I_{2 \text{ pre DY}}}}$$

## 2.7. Statistical analyses

The analyses of growth indices and climate attributes *ms* (1998–2012), *Rs*, *Rc* and *Rl* were done with R software. We used linear regressions to account for growth variability with increasing stem height. Differences between tree species within height or volume sections as well as between drought years were assessed by analyses of variance (ANOVA) and the non-parametric Kruskal-Wallis test by rank, since homogeneity of variance of residuals or normal distribution of the values were not given for *ms*, *Rs*, *Rc*, and *Rl*. Post hoc analyses were conducted by Dunn's multiple comparison test with Holm-Šidák adjustment (R package *dunn.test*; Dinno, 2016). Assuming that total stem volume increment ( $VI_{TS}$ ) represents the aboveground stem wood production most accurately, we used  $VI_{TS}$  measures as a reference for all attributes (such as *ms*, *Rs*, *Rc* and *Rl*) for species description. Due to mutual dependencies of different height and volume sections extracted from identical trees, paired *t*-tests and Wilcoxon tests were performed to detect differences between  $BAI_{1.3}$  and  $VI_{TS}$  as well as  $VI_{LS}$  and  $VI_{US}$ ,

respectively.

The variability in *ms*, *Rs*, *Rc*, and *Rl* with stem height was quantified separately by a set of univariate regression analyses according to (Allan et al., 2014; see also Fig. 1). A total of six basic models were fitted individually in order to derive species-specific response shapes (Table A.3). We used tree number as a fixed effect on the intercept, and subsequently averaged intercepts for each species. The applied functions included a null model, without response dependencies from tree height (or with the sole effect of tree number); polynomial models up to second order, representing linear and quadratic (one turning point) relationships; and three additional nonlinear models: negative exponential, asymptotic exponential and power law regression models (Crawley, 2013). For evaluation of the goodness-of-fit and model selection, we compared different models based on AICc (Akaike's Information Criterion, corrected for small sample sizes) according to Burnham and Anderson (2010). Furthermore, pseudo- $R^2$  was calculated using the square of Pearson's correlation coefficient between observed values and predicted estimators fitted by the model. Shape modelling and computations were performed using the R packages *nlme* (Pinheiro et al., 2016), *nls2* (Grothendieck, 2013) and *pgirmess* (Giraudoux, 2016).

## 3. Results

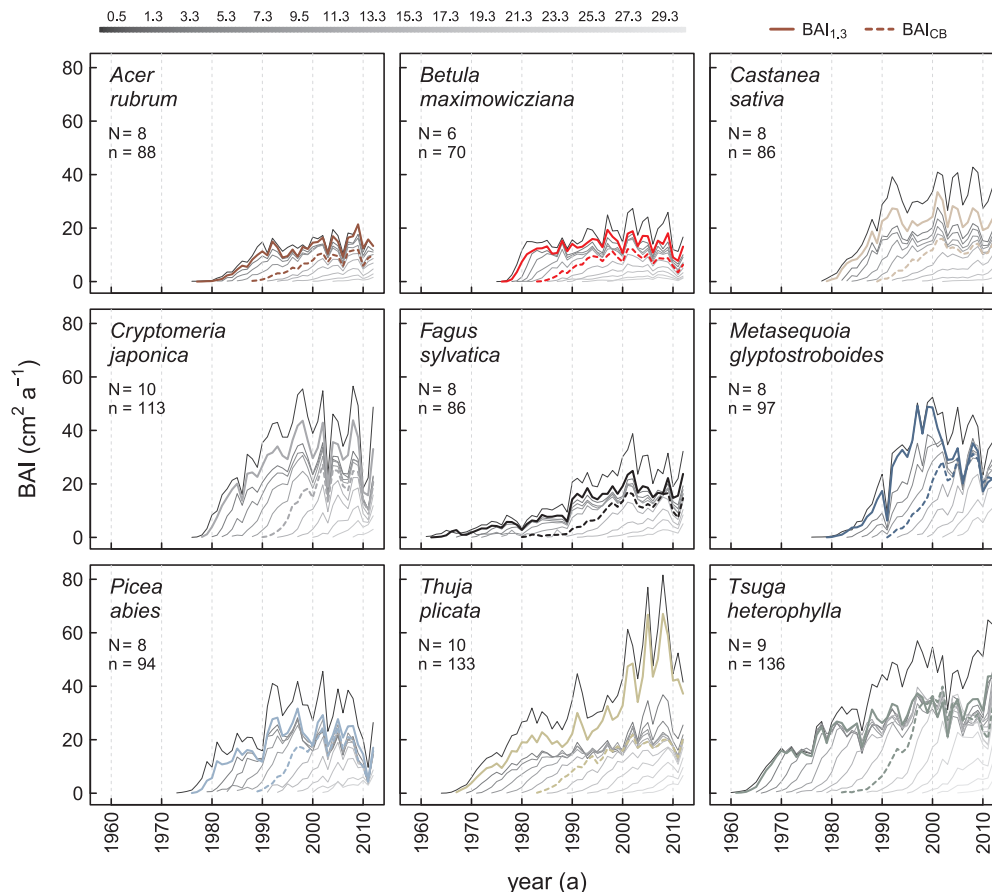
### 3.1. Dendrometric growth characteristics

We found distinct differences in annual increments and growth patterns (culmination and growth trend) amongst the tree species (Fig. 2). Mean radial increment (referring to the life span of individual species) at breast height ( $RI_{1.3}$ ) varied significantly from 2.7 mm (*Fagus*), 3.1 mm (*Acer*), 3.3 mm (*Betula*) and 3.9 mm (*Picea*, *Tsuga*) to 4.2 mm (*Thuja*), 4.3 mm (*Castanea*), 4.9 mm (*Cryptomeria*) and 5.0 mm (*Metasequoia*;  $p < 0.001$ , Table A.2). Basal area increment at breast height ( $BAI_{1.3}$ ) as well as height and volume increment ( $HI_{TS}$  and  $VI_{TS}$ ) differed strongly among tree species ( $p < 0.001$ , Table A.2). Across different height sections, an early culmination of BAI values was observed for the species *Acer*, *Betula*, *Castanea* and *Metasequoia* (and to some extent *Picea*) after around 20 to 25 years. However, BAI of *Fagus*, *Thuja* and *Tsuga* reached their maxima markedly later, indicating a strong dependency of age-related growth trends on species, and underlining the importance of detrending.

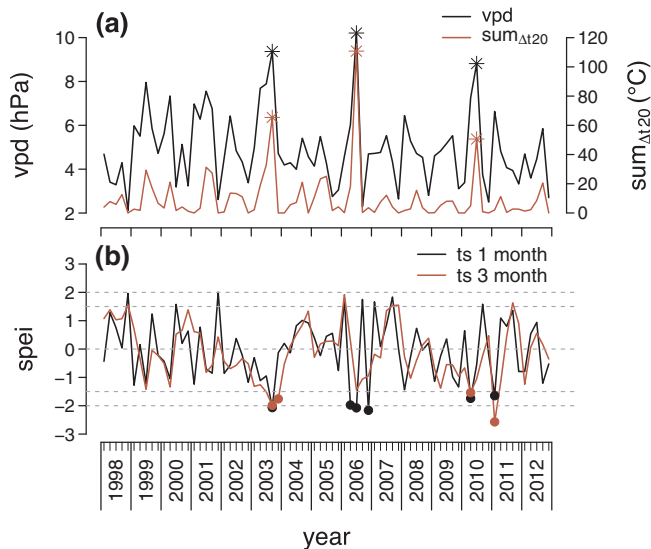
### 3.2. Stress events and chronology characteristics

For the common period 1998–2012, we identified three years with pronounced high *vpd* and degree day sums significantly above the 15-year average during the growing season (95% quantile *vpd* = 7.96 hPa; 95% quantile  $\text{sum}_{\Delta t 20} = 31.78^\circ\text{C}$ ) signifying high transpiration and heat accumulations in August of 2003 and July of 2006 and 2010 (Fig. 3a). Simultaneously, the same years and additionally the year 2011 reflected severe and extreme water deficits, as shown by low *spei* values (below -1.5 and -2.0, Fig. 3b). 2003, 2010 and 2011 were characterized by a) abrupt drought in single month (August 2003, June 2010 and May 2011) and b) persistent 3-month drought (June–August and July–September 2003, April–June 2010 and March–May 2011). However, fluctuating short-term (1-month) conditions with strong water deficits (June, July and September) and high water supply (May and August) dominated the year 2006.

The stress events of 2003, 2006, and 2010 corresponded with growth depressions for all tree species (except for *Picea* in 2010, Fig. 4). In contrast to the majority of species, no additional decline could be found in the growth indices of *Acer*, *Castanea*, *Metasequoia* and *Tsuga* trees during 2011. Furthermore, slight increases in the lower BAI indices ( $BAI_{0.5}$  and/or  $BAI_{1.3}$ ) were found for *Betula*, *Cryptomeria*, *Fagus* and *Thuja* in 2011. To take the successive droughts spanning the years 2010 and 2011 into account, growth was averaged for these two years



**Fig. 2.** Species-specific basal area increment (BAI) chronologies at different sampling heights (0.5–29.3 m). The coloured lines indicate chronologies at breast height (BAI<sub>1.3</sub>) and at the nearest mean crown base height (BAI<sub>CB</sub>). N = number of trees, n = number of stem disks.



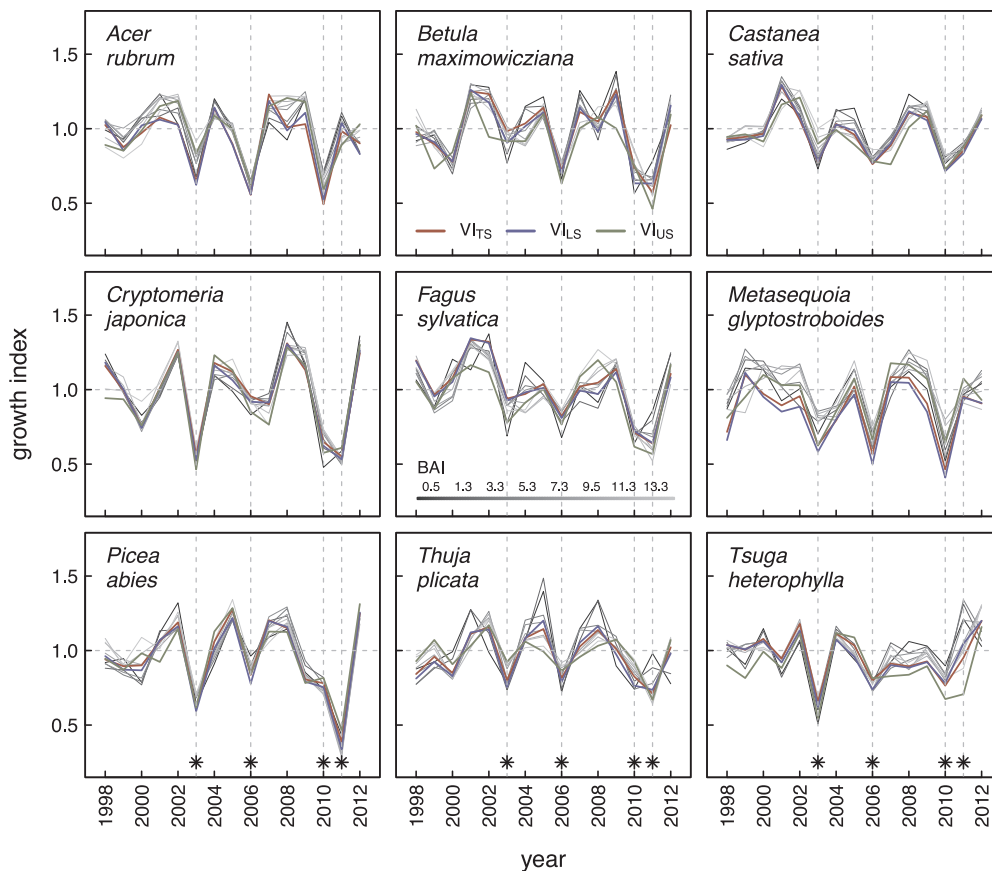
**Fig. 3.** (a) Vapour pressure deficit (vpd), degree day sum ( $sum_{\Delta 20}$ ), given as sum of the differences in temperatures  $> 20^{\circ}\text{C}$  and  $20^{\circ}\text{C}$  and (b) standardized precipitation evapotranspiration index (spei) for the growing season (May–September) from 1998 to 2012, calculated for 1-month and 3-month (spanning from two previous to current month) timescales (ts, black and red lines). Asterisks indicate years with high levels in vpd and  $sum_{\Delta 20}$ , points mark severe ( $spei < -1.5$ ) and extreme ( $spei < -2.0$ ) drought events.

for further analysis of *resistance* ( $R_s$ ), *recovery* ( $R_c$ ) and *resilience* ( $R_l$ ). Here,  $R_c$  and  $R_l$  indices referred to 1-year post-drought period (2012) as stem disks of *Betula* and *Cryptomeria* were sampled in summer 2013 (annual increment not completed in 2013; cf. Table A.1).

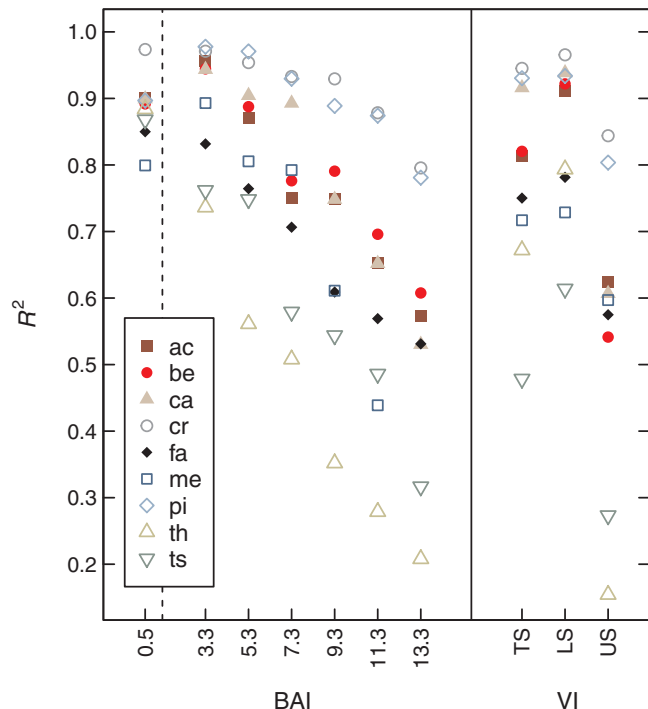
The statistical attributes  $es$  (effective chronology signal) and  $eps$  (expressed population signal) exceeded threshold values for all height chronologies (overall range:  $es = 0.431\text{--}0.846$ ,  $eps = 0.857\text{--}0.982$ ) indicating reliable and noise-free chronology quality concerning the comparability with numerous former studies (shown for BAI<sub>1.3</sub>, VI<sub>TS</sub>, VI<sub>LS</sub> and VI<sub>US</sub> in Table A.4). Within species, individual height chronologies were strongly and positively correlated with each other (data not shown). However, both BAI and VI variables' correlation with increasing distance between stem heights decreased (Fig. 5). Linear regressions revealed that BAI<sub>1.3</sub> measures explained 48% (*Tsuga*) to 95% (*Cryptomeria*) of VI<sub>TS</sub> variance and 61% (*Tsuga*) to 97% (*Cryptomeria*) of VI<sub>LS</sub> variance, respectively ( $p < 0.05$ ). For *Thuja* trees, upper stem VI<sub>US</sub> and BAI<sub>13.3</sub> variance (15% and 21%) could not be explained by BAI<sub>1.3</sub>.

### 3.3. Mean sensitivity and variation with stem height

Mean sensitivity ( $ms$ ), calculated as year-to-year variation in individual trees, was strongly affected by tree species for the growth variables BAI<sub>1.3</sub>, VI<sub>TS</sub>, VI<sub>LS</sub> and VI<sub>US</sub> ( $p < 0.01$ , Table 1). Highest  $ms$  was found for *Cryptomeria* and *Picea* trees, indicating that the growth of these species was strongly controlled by climatic factors. We determined low sensitivity for *Castanea*, *Thuja* and *Tsuga* whereas *Acer*, *Betula*, *Fagus* and *Metasequoia* could be considered as moderately sensitive to external impacts. However, the number of significant differences between species ( $n_{\text{sign}}$ ) varied among growth variables (Dunn



**Fig. 4.** Standardized basal area and volume increment (BAI and VI) chronologies at different height (BAI<sub>0.5</sub> to BAI<sub>13.3</sub>) and volume (VI<sub>TS</sub>, VI<sub>LS</sub>, VI<sub>US</sub>) sections. Asterisks indicate stress events corresponding to high *vpd* and *sum*<sub>Δt20</sub> and low *spei* values simultaneously. 0.5–13.3 = 0.5 m to 13.3 m stem height; TS = total stem, LS = lower stem section below crown base height, US = upper stem section above crown base height.



**Fig. 5.** Relationships between standardized BAI<sub>1.3</sub> (dashed line) and BAI or VI chronologies of various height sections for the period 1998–2012 ( $R^2$ ; except for *Thuja* BAI<sub>1.3</sub> and VI<sub>US</sub>, all  $p < 0.05$ ;  $N = 6–10$ ). BAI = basal area increment, VI = volume increment, 0.5–13.3 = 0.5 m to 13.3 m stem height; TS = total stem, LS = lower stem, US = upper stem, ac = *Acer*, be = *Betula*, ca = *Castanea*, cr = *Cryptomeria*, fa = *Fagus*, me = *Metasequoia*, pi = *Picea*, th = *Thuja*, ts = *Tsuga*.

test,  $p < 0.05$ ). The comparably fewer differences in BAI<sub>1.3</sub> variables indicate that sensitivities at breast height were more similar among species when compared with volume increment variables (VI<sub>TS</sub>, VI<sub>LS</sub>, VI<sub>US</sub>).

Within species, *ms* differed strongly as a function of stem height and growth variable (BAI and VI; Table 1). For all species, BAI<sub>1.3</sub> sensitivity exceeded VI<sub>TS</sub> measures by 0.2–56.2% and significant differences were calculated for six of the nine species (paired *t*-test and Wilcoxon test,  $p < 0.05$ ). Comparisons between lower and upper VI portions showed a more homogeneous pattern, which was significantly different for only three species.

Our analyses of height-sensitivity relationships (0.5 m to 13.3 m) indicated species-specific responses of *ms* to stem height (Fig. 6). For all species, inter-annual variation followed a decreasing trend with increasing tree height, with reduction in *ms* by 7.2% (*Picea*) to 48.7% (*Thuja*). While *Acer*, *Castanea*, *Cryptomeria*, *Metasequoia*, *Picea* and *Tsuga* showed a uniform decline, *ms* reduction was even more pronounced in the lower sections of *Betula*, *Fagus* and *Thuja* when considered longitudinally.

#### 3.4. Response to heat-related drought

An overview for species-specific responsiveness to stress events is presented for the total stem volume increment (VI<sub>TS</sub>) since this variable incorporated several tree height sections and, thus, representing trees growth reaction most reliable (a summary of the drought response indices for the major growth variables BAI<sub>1.3</sub>, VI<sub>TS</sub>, VI<sub>LS</sub> and VI<sub>US</sub> is provided in Table A.5). We found significant differences among tree species for all tolerance components and drought years ( $p < 0.001$ , Fig. 7a, Table 2). The highest variation between years in *resistance* (*Rs*), *recovery* (*Rc*) and *resilience* (*Ri*) based on VI<sub>TS</sub> was identified for *Cryptomeria* (coefficient of variation, *cv* = 0.31 for *Rs*, *cv* = 0.28 for *Rc*, difference between stress events  $\Delta$ DI:  $p < 0.001$ ) and *Tsuga* (*cv* = 0.20

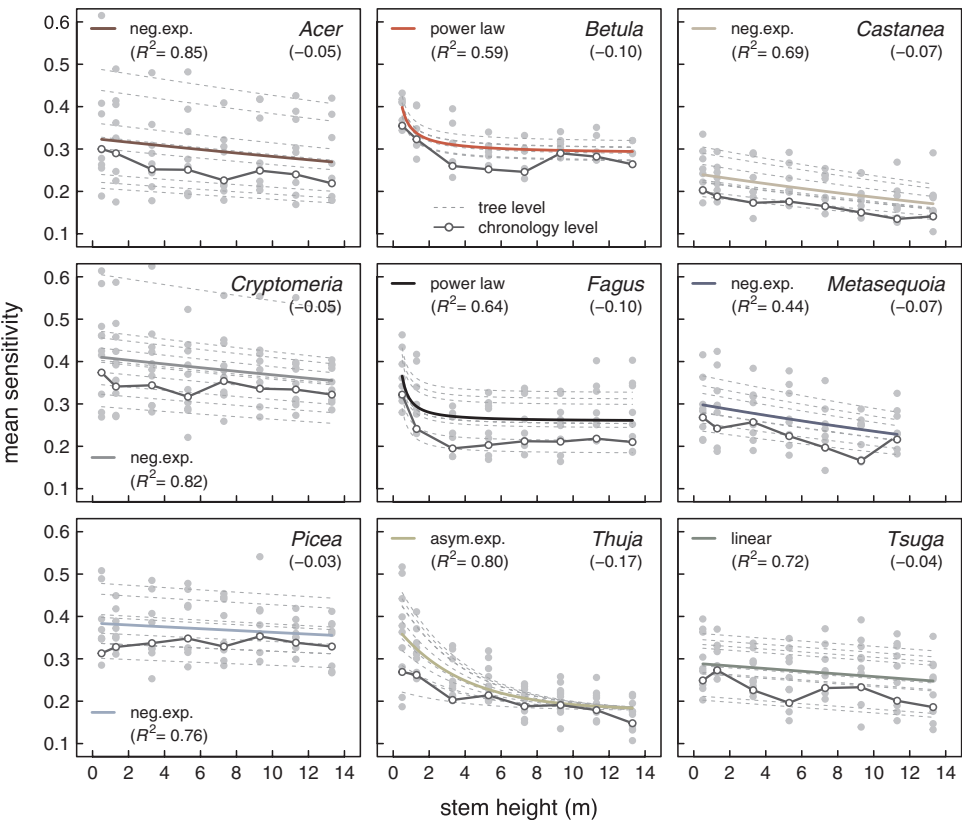
**Table 1**  
Mean sensitivity (*ms*) of tree species for different growth variables and height sections (BAI<sub>1.3</sub>, VI<sub>TS</sub>, VI<sub>LS</sub>, VI<sub>US</sub>) within the period 1998–2012. Letters indicate significant differences between tree species within a considered section, calculated with Dunn’s multiple comparison test and Holm–Šidák adjustment (Dunn,  $p < 0.05$ ,  $df = 5–9$ ). Kruskal–Wallis tests resulted in significant effects of the factor *tree species* on *ms* for all variables ( $df = 8$ ). Paired *t*-tests and Wilcoxon-tests were implemented for comparison of sensitivities of BAI<sub>1.3</sub> with VI<sub>TS</sub> as well as of VI<sub>LS</sub> with VI<sub>US</sub> ( $p < 0.001$  \*\*\*,  $p < 0.01$  \*\*,  $p < 0.05$  \*).

Species	BAI <sub>1.3</sub>	VI <sub>TS</sub>	BAI <sub>1.3</sub> vs VI <sub>TS</sub>	VI <sub>LS</sub>	VI <sub>US</sub>	VI <sub>LS</sub> vs VI <sub>US</sub>
	Dunn	Dunn	paired	Dunn	Dunn	paired
<i>Acer rubrum</i>	0.33 <sup>ab</sup>	0.33 <sup>bc</sup>		0.35 <sup>cd</sup>	0.28 <sup>abcd</sup>	***
<i>Betula maximowicziana</i>	0.34 <sup>ab</sup>	0.27 <sup>abc</sup>	*	0.30 <sup>abcd</sup>	0.31 <sup>abc</sup>	
<i>Castanea sativa</i>	0.23 <sup>a</sup>	0.21 <sup>a</sup>	*	0.22 <sup>a</sup>	0.20 <sup>ad</sup>	
<i>Cryptomeria japonica</i>	0.40 <sup>b</sup>	0.36 <sup>b</sup>	*	0.39 <sup>c</sup>	0.37 <sup>b</sup>	
<i>Fagus sylvatica</i>	0.32 <sup>ab</sup>	0.26 <sup>abc</sup>	*	0.25 <sup>abcd</sup>	0.29 <sup>abc</sup>	
<i>Metasequoia glyptostroboides</i>	0.30 <sup>ab</sup>	0.30 <sup>abc</sup>		0.32 <sup>bcd</sup>	0.28 <sup>abcd</sup>	
<i>Picea abies</i>	0.37 <sup>b</sup>	0.36 <sup>b</sup>		0.39 <sup>c</sup>	0.32 <sup>bc</sup>	**
<i>Thuja plicata</i>	0.32 <sup>ab</sup>	0.21 <sup>a</sup>	***	0.23 <sup>ab</sup>	0.17 <sup>d</sup>	**
<i>Tsuga heterophylla</i>	0.30 <sup>ab</sup>	0.22 <sup>ac</sup>	*	0.23 <sup>abd</sup>	0.24 <sup>acd</sup>	
total ( <i>n</i> <sub>sign</sub> )	2	8	6	9	7	3
Kruskal–Wallis						
χ <sup>2</sup>	23.8	41.2		43.2	41.5	
<i>p</i> -value	0.002	< 0.001		< 0.001	< 0.001	

BAI = basal area increment, VI = volume increment, 1.3 = 1.3 m stem height, TS = total stem, LS = lower stem, US = upper stem, *n*<sub>sign</sub> = number of significant differences.

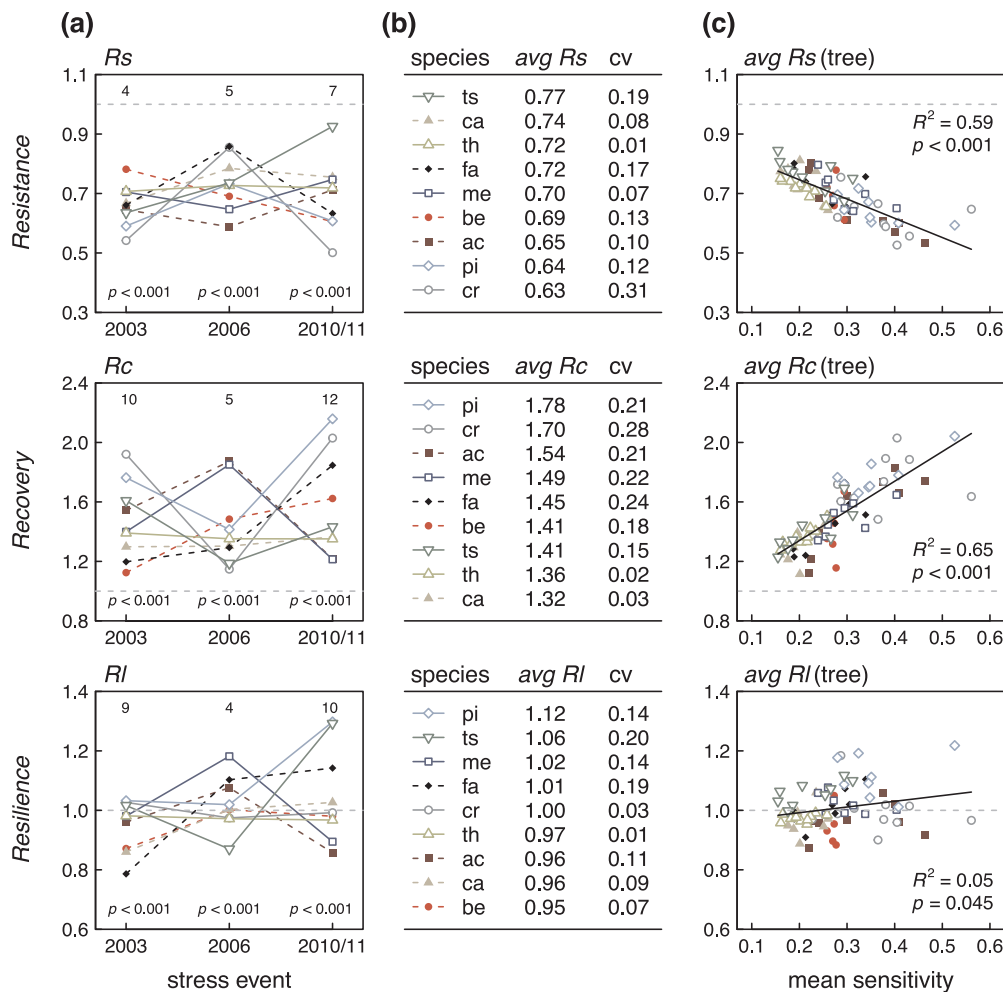
for *R<sub>L</sub>*, ΔDY:  $p < 0.001$ , Fig. 7b, Table 2). Accordingly, *Cryptomeria* yielded the highest *ms* values (confer Table 1). The lowest variations between drought years were found for *Thuja* trees for all tolerance indices ( $cv = 0.01–0.02$ ). Concerning *R<sub>s</sub>*, growth depressions ranged from 12% (*Betula*) to 46% (*Cryptomeria*) in 2003, 14% (*Cryptomeria*, *Fagus*) to 41% (*Acer*) in 2006 and 7% (*Tsuga*) to 50% (*Cryptomeria*) in 2010/11. Looking at pooled *R<sub>s</sub>* across stress events (*avg R<sub>s</sub>*), *Tsuga* and *Castanea* exhibited lowest growth reduction, while high declines were found for *Cryptomeria*, *Picea* and *Acer* (Fig. 7b). In contrast, *R<sub>c</sub>* values of *Picea* and *Cryptomeria* were highest across drought years (*avg R<sub>c</sub>*). Here, low increment values of *Castanea*, *Thuja* and *Tsuga* in the two-year period

after droughts reflected a minor recovery on average. Values of *R<sub>L</sub>* ranged from -21% (*Fagus*) to 3% (*Cryptomeria* and *Picea*) in 2003, -13% (*Tsuga*) to 18% (*Metasequoia*) in 2006 and -14% (*Acer*) to 30% (*Tsuga*) in 2010/11. As a result, *avg R<sub>L</sub>* across drought years was highest for *Picea* and *Tsuga* and lowest for *Betula*, *Castanea*, *Acer* and *Thuja*. For the pooled response indices *R<sub>s</sub>* and *R<sub>c</sub>* of individual trees (*avg R<sub>s</sub>* [tree] and *avg R<sub>c</sub>* [tree]), we found close relationships between mean sensitivity (1998–2012) and drought tolerance components ( $p < 0.001$ ) indicating a lower *R<sub>s</sub>* and higher *R<sub>c</sub>* of more sensitive species and an opposite pattern for less sensitive species (Fig. 7c). Lower relationships were found for *avg R<sub>L</sub>* (tree) and *ms* ( $p = 0.045$ ).



**Fig. 6.** Response of tree species’ mean sensitivity (*ms*) to stem height for the period 1998–2012. *Ms* was calculated on the base of detrended basal area increment (BAI) series of the 8 lower height sections (BAI<sub>0.5</sub> to BAI<sub>13.3</sub>), except *Metasequoia* with 7 height sections (BAI<sub>0.5</sub> to BAI<sub>11.3</sub>). For each species, prediction of the best-fitted model (null, linear, quadratic, neg.exp., asym.exp., power law; solid coloured line) according to AICc are shown. Grey dashed lines indicate first model fits of single trees with only different intercepts. Changes in *ms* were calculated as the difference between *ms* at lowest (0.5 m) and highest (13.3 m or 11.3 m) stem height, both predicted by the first model, and are shown in brackets. Additionally, *ms* values of the BAI height chronologies are marked by linked points.  $R^2$  = pseudo- $R^2$ , neg.exp. = negative exponential, asym.exp. = asymptotic exponential.  $N = 6–10$ .





**Fig. 7.** (a) Drought response indices resistance ( $R_s$ ), recovery ( $R_c$ ) and resilience ( $R_l$ ) of detrended volume increment ( $VI_{TS}$ ) for the stress events in 2003, 2006 and 2010/11, calculated as means of  $N = 6$ –10 trees per species. Kruskal-Wallis tests resulted in significant differences between tree species ( $p < 0.001$ ,  $df = 8$ ). Values above points indicate numbers of significant differences ( $n_{sign}$ ) between species for the given observation unit (Dunn's multiple comparison test and Holm-Šidák adjustment,  $p < 0.05$ ). Lines between different stress events highlight the variability in responses within each deciduous (dashed line) and coniferous (solid line) tree species. (b) Pooled average indices ( $avg R_s$ ,  $avg R_c$  and  $avg R_l$ ; presented in descending order) and coefficient of variation ( $cv$ ) across the event years ( $N = 3$ ). (c) Linear relationships of pooled average indices across the stress events ( $avg R_s$  [tree],  $avg R_c$  [tree] and  $avg R_l$  [tree]) and mean sensitivity (1998–2012) for individual trees ( $N = 6$ –10). ac = *Acer*, be = *Betula*, ca = *Castanea*, cr = *Cryptomeria*, fa = *Fagus*, me = *Metasequoia*, pi = *Picea*, th = *Thuja*, ts = *Tsuga*.

### 3.5. Relationships between stem height and drought response in 2003 (shape modelling)

Within tree species, we identified differing shapes of drought response with varying stem height that differed among stress events. To analyse intra-species variability, tree shapes are shown for the

extraordinary trans-European heatwave in 2003 (Beniston, 2004; Ciais et al., 2005; for differences in the years 2006 and 2010/11 see Table A.5). Here, growth response to drought in terms of  $BAI_{1.3}$  reflected the reaction of  $VI_{TS}$  for several species (Fig. 8a). However, for the majority of species,  $BAI_{1.3}$  led to tendentially lower  $R_s$  and higher  $R_c$  or higher  $R_l$  when compared with  $VI_{TS}$  values. Pairwise comparisons resulted in

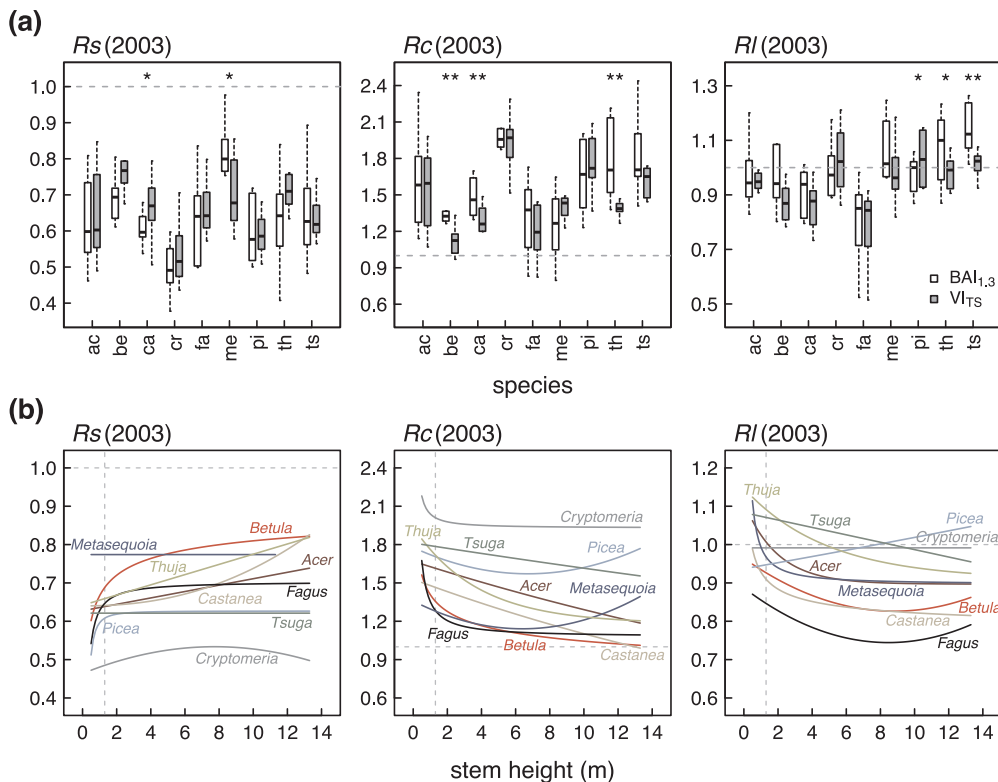
**Table 2**

Significant differences in the response indices resistance ( $R_s$ ), recovery ( $R_c$ ) and resilience ( $R_l$ ) between tree species (Dunn test and Holm-Šidák adjustment,  $p < 0.05$ ,  $df = 5$ –9) and between the stress events in 2003, 2006 and 2010/11 ( $\Delta DY$ ; Kruskal-Wallis test,  $p < 0.001$  \*\*\*,  $p < 0.01$  \*\*,  $p < 0.05$  \*,  $df = 2$ ), calculated for the detrended volume increment ( $VI_{TS}$ ) and presented in ascending order of  $p$ -value.

Index	Stress event (DY)			$\Delta DY$	
	2003	2006	2010/11		
$R_s$	be > cr, pi	cr > ac, me, be	ts > cr, pi, be, fa	***	cr, ts
	th > cr	fa > ac, me	ca > cr	**	fa
			me > cr	*	be
	me > cr		th > cr		
$R_c$	cr > be, fa, ca, th, me	me > cr, ts, fa	pi > ac, me, th, ca, ts	***	cr, me, pi, fa
	pi > be, fa, ca	ac > cr, ts	cr > ac, me, th, ca, ts	**	ts, ac
	ts > be, fa		fa > ac, me	*	be
$R_l$	ts > fa, ca, be	me > ts, th, cr	ts > me, ac, th, cr, be	***	ts, me
	cr > fa, ca	ac > ts	pi > me, ac, be	**	fa, ac
	pi > fa, ca		fa > ac, me	*	pi, ca
	th > fa				
	me > fa				

ac = *Acer*, be = *Betula*, ca = *Castanea*, cr = *Cryptomeria*, fa = *Fagus*, me = *Metasequoia*, pi = *Picea*, th = *Thuja*, ts = *Tsuga*.





**Fig. 8.** Relationships between growth variable or stem height and drought response indices *resistance* ( $R_s$  [2003]), *recovery* ( $R_c$  [2003]) and *resilience* ( $RI$  [2003]) for the stress event in 2003. (a) Comparison of response indices based on detrended basal area increment at breast height ( $BAI_{1.3}$ ) and detrended volume increment ( $VI_{TS}$ ). Asterisks indicate significant differences between growth variable  $BAI_{1.3}$  and  $VI_{TS}$  within considered species, implemented by paired *t*-tests and Wilcoxon tests ( $p < 0.01$  \*\*,  $p < 0.05$  \*;  $N = 6-10$ ). ac = *Acer*, be = *Betula*, ca = *Castanea*, cr = *Cryptomeria*, fa = *Fagus*, me = *Metasequoia*, pi = *Picea*, th = *Thuja*, ts = *Tsuga*. (b) Best model fits of response of  $R_s$ ,  $R_c$  and  $RI$  to stem height. Drought response indices were calculated on the basis of detrended basal area increment (BAI) series of the lower 8 height sections ( $BAI_{0.5}$  to  $BAI_{13.3}$ ), except for *Metasequoia* with 7 height sections ( $BAI_{0.5}$  to  $BAI_{11.3}$ ). Model predictions of the best-fitted models (null, linear, quadratic, negative exponential, asymptotic exponential, power law) according to AICc ( $\Delta AICc < 2$ ) are provided for each species.

significantly lower  $R_s$  indices of  $BAI_{1.3}$  for *Castanea* but higher  $R_s$  values of  $BAI_{1.3}$  for *Metasequoia*. Contrasting patterns were found for  $R_c$  indices, indicating a significantly higher  $R_c$  at breast height for *Betula*, *Castanea* and *Thuja*. Likewise, less distinct differences could be found for  $RI$  indices, and *Picea* proved to be less resilient and the species *Thuja* and *Tsuga* more resilient at  $BAI_{1.3}$  level when compared with  $VI_{TS}$ .

Regression analysis of BAI measurements revealed a positive response of  $R_s$  with increasing stem height for most tree species (Fig. 8b). *Betula*, *Fagus* and *Picea* appeared to be strongly affected by the drought at lowest height sections, while  $R_s$  of *Acer*, *Castanea*, and *Thuja* increased more constantly. The greatest changes in  $R_s$ , calculated as the ratio of  $R_s$  ( $\Delta R_s$ ), predicted by the model at the uppermost stem height (13.3 m) and the minimum height (0.5 m), were found for *Betula* ( $\Delta R_s = 37\%$ ), *Castanea* and *Fagus* ( $\Delta R_s = 29\%$ , Table A.6). However, no such trend was found for *Metasequoia* and *Tsuga* trees. In contrast,  $R_c$  indices decreased with increasing height (by on average 27%) except in the case of *Picea* and *Metasequoia*.  $RI$  values decreased with increasing height sections for *Acer*, *Betula*, *Castanea*, *Fagus*, *Thuja* and *Tsuga* (by on average 13%), whereas the resilience of the other species was constant (*Cryptomeria*) or increasing (*Metasequoia*, *Picea*) with greater stem heights.

#### 4. Discussion

Our analyses of growth variation confirmed that annual wood formation by alien and native tree species differed species-specifically under the same site conditions, that are favourable for forest growth (due to high precipitation and moderate winter temperatures). All species exhibited simultaneous declines in basal area and volume increment during drought and heat events, but the magnitude in growth depression strongly differed among tree species. Furthermore, inconsistencies in the growth responses of the different tree species across dry years indicate that the growth response of a species depends on the type and intensity of a drought event.

##### 4.1. Quantification of drought conditions

Our findings suggest that a) different temporal scales of climate variables and b) both precipitation- and temperature-driven predictors should be considered when identifying and quantifying drought stress.

To evaluate drought events, most growth studies have focused on longer periods of water shortage (spanning three months at least; Mette et al., 2011). However, our study confirmed the findings of George et al. (2015) who pointed out the importance of short-term variability (e.g. 1 month) for tree growth dynamics. The low (raw and detrended) growth values in the year 2006 of all investigation species emphasize that frequent and intensive temporary water deficits across the vegetation period (in June, July and September) affect patterns of annual increment of both sensitive and less sensitive tree species. The high water supply (in May and August of 2006) was not sufficient to facilitate species recovery in the same year. Besides short-term events, an intensive and long-lasting summer drought in 2003 and persisting dryness in springs of 2010 and 2011 also impacted tree growth species-specifically. In comparison, a lower resistance to short-term drought (2006) could be observed for *Acer* and *Metasequoia*, and *Cryptomeria*, *Fagus* and *Picea* were found to be less resistant to persistent drought (2003, 2010/11; Fig. 7a).

The exceptionally high  $v_{pd}$  and  $sum\Delta_{t20}$  values in August (2003) and July (2006 and 2010) indicated strong summer heat inducing physiological stress caused by high evaporative water demand (Bouriaud et al., 2005; Will et al., 2013). In contrast, the more balanced  $v_{pd}$  in 2011 suggested that trees may have maintained stomatal conductance. We found that  $v_{pd}$  was largely controlled by the maximum temperature (linear regression:  $R^2 = 0.58$ ,  $p < 0.001$ ), the primary trigger of persistent drought and suitable for predicting drought tolerance (Williams et al., 2012). We therefore conclude that the additional consideration of mainly temperature-driven predictors (such as  $v_{pd}$  and heat sums) may improve the capabilities to derive species-specific growth responses to drought conditions.

In total, as reported by Bhuyan et al. (2017), the selection of  $spei$  at 1- and 3-month timescale seem to be an appropriate choice at Burgholz

site since tree growth of temperate forests is expected to be primarily sensitive to short- and medium-term drought. However, this study focuses on drought conditions during the current growing season, and responses to previous dry periods were not considered. To account for the direct impact of individual climate predictors at defined (stationary and moving) periods for the whole lifespan of the investigation trees, further growth-climate correlation analyses are required.

#### 4.2. Species-specific differences in drought response and implications for alien and native species

In this study, we applied the growth indices *resistance*, *recovery* and *resilience* of the whole stem ( $VI_{TS}$ ) for defined drought events giving the most general (concerning the variation along the stem) and comparable (concerning growth traits during and after drought) insight of species' drought tolerance at our study site. *Cryptomeria*, *Picea* and *Acer* were least resistant and *Tsuga* and *Castanea* showed highest resistance; *Thuja*, *Fagus*, *Metasequoia* and *Betula* were in an intermediate position. In contrast, *Castanea* and *Thuja* recovered slowly while *Picea* and *Cryptomeria* indicated highest, and *Acer*, *Metasequoia*, *Fagus*, *Betula* and *Tsuga* moderate recovery after drought (Fig. 7b). Hence, trade-offs between resistance and recovery or resilience were not uniform among tree species, i.e. species with high growth reduction did not necessarily reveal a greater recovery. For a general ranking of drought tolerance,  $R_s$  seems to be the most expressive variable as highly resistant species have no need to recover or to be resilient as much as species of lower  $R_s$  (Kunz et al., 2018). Across stress events, this growth susceptibility to drought was highly correlated to species' inter-annual growth variation (specified by  $ms$ ) indicating a stronger drought response of highly sensitive species (Fig. 7c). Hence,  $ms$  is a useful measure for quantifying tolerances to diverging drought disturbances and should be considered for ranking of drought sensitivity at homogenous site conditions (Feliksik and Wilczyński, 2009; Wilczyński et al., 2014). Here, *Cryptomeria* and *Picea* revealed highest, and *Castanea*, *Thuja* and *Tsuga* lowest  $ms$ . The variation of drought responses between the species and drought years indicate species-specific tolerance to drought events of varying intensity or different timing during the growing season (Fig. 7a).

These differences may result from specific demands (for soil and climate) and **long-term adaptation** due to the climatic conditions of their natural distribution (Bolte et al., 2009; Millar et al. 2007). For *Cryptomeria japonica*, originating from isolated areas of the cool-temperate, humid climate in Japan (Shen, 1999), a strong sensitivity to atmospheric water deficits (Tange et al., 2009) is well known. The comparable low resistance (2003, 2010/11) could be related to its demand for constantly high humidity of the (sub-)montane zone, where long-lasting periods of dryness lacking (Shen 1999). Likewise, native *Picea abies* prefers high precipitation sums at higher altitude and has been classified as a European species vulnerable to presumed climatic impacts such as spring or summer drought (e.g. Kölling et al., 2009; Lebourgeois et al., 2010; Lévesque et al., 2013; Pretzsch et al., 2013; Vitali et al., 2017). Interestingly, both species, *Picea* and *Cryptomeria*, are characterized by shallow root systems (Konôpka et al., 2006; Schmid and Kazda, 2002) and in our study exhibited remarkably similar growth and response characteristics (Figs. 4, 6 and 7a). In contrast, the western North American *Thuja plicata* and *Tsuga heterophylla* are distributed under (largely comparable) broad ecological amplitudes with maritime influence (e.g. Antos et al., 2016; Burns and Honkala, 1990). Additionally, for both species, a great abundance on moist and nutrient-poor sites (Antos et al., 2016) is largely consistent to the conditions of the study site (cf. 2.1). This may explain the observed high  $R_s$  for the individual drought events at favourable site conditions for study trees (Fig. 7a, b). For *Thuja*, high stress tolerance under a wide ecological range (high survival rates on productive sites and persistence under adverse conditions; Antos et al., 2016), especially a high resistance to summer drought (Grossnickle and Russell, 2010), has been reported. The weak sensitivity of *Tsuga* to climatic fluctuations is in line with the

findings of Ettinger et al. (2011). For European native *Fagus sylvatica*, with wide distribution in Central and Western Europe of the temperate and warm-temperate zones, conditions of the study site Burgholz seem to be favourable with respect to climatic (mild temperature and high precipitation amount) and soil properties (e.g. Felbermeier and Mosandl, 2002). The comparable high  $R_s$  of study trees may therefore indicate a higher adaptive potential. With respect to drought sensitivity, several studies have been published (for an overview see, for example, Knutzen et al., 2017). Hence, *Fagus* has been found to be moderately sensitive (van der Werf et al., 2007; Zang et al., 2014) or vulnerable to droughts (e.g. Bréda et al., 2006; Dulamsuren et al., 2017; Weber et al., 2013; Zimmermann et al., 2015). For the remaining species, no relationships between drought response of study trees and its origin characteristics could be found. This in particular applies for the eastern North American generalist *Acer rubrum* (Abrams 1998). Its huge ecological amplitude (with highest climate tolerance within the genus *Acer*; Walters and Yawney, 1990), low resource requirements and high adaptive (physiological and morphological) potentials (Abrams 1998; Hart et al., 2012) could have been expected to reveal lower drought response. In fact, a low  $R_s$  and, additional, rather moderate  $R_c$  of the study trees does not coincide with generalist characteristics (Fig. 7a, b).

Another explanation for the differences in drought response between the tree species could be linked to **physiological strategies** to regulate water stress during drought (McDowell et al., 2008). For summary, two general mechanisms for water regulation have been described: isohydric and anisohydric. According to recent literature the species *Acer* (Thomsen et al., 2013), *Cryptomeria* (Kumagai et al., 2009), *Metasequoia* (Brodribb et al., 2014; Chen et al., 2012), *Picea* (e.g. Hartl-Meier et al., 2015; Klein and Niu, 2014; Zang et al., 2014), *Thuja* (McCulloh et al., 2014; Warren et al., 2003) and *Tsuga* (McCulloh et al., 2014) were classified to follow isohydric hydraulic behaviour. For this species, stomatal closure in early stages of water stress results in carbon starvation and lower wood productivity (low  $R_s$ ), especially during persistent drought periods (Gebhardt et al., 2014; Hartmann, 2011; McDowell et al., 2008). One the other hand, these species are able to prevent damage to essential organs (leaves and fine roots) and hence, growth can be resumed quickly (high  $R_c$ ; Pretzsch et al. 2013). For the intensive, long-lasting (2003) and successive (2010/11) droughts this particularly holds for *Cryptomeria* and *Picea* given by strong growth declines during ( $R_s = 0.50$ – $0.61$ ) and high recovery in the years after drought ( $R_c = 1.76$ – $2.16$ ; Fig. 7a). For the widely cultivated Chinese *Metasequoia glyptostroboides* (Williams, 2005), and also for *Acer*, the isohydric character might explain the stress reaction in 2006: during drought, growth ceased quickly ( $R_s = 0.59$  and  $0.65$ ) and the stored resources could be used for faster recovery after stress ( $R_c = 1.87$  and  $1.85$ ). In contrast to our findings (moderate drought-tolerant, given by intermediate  $R_s$  and  $R_c$  for individual drought events; Fig. 7a, b), *Metasequoia* has been classified as a sensitive (Wilczyński et al., 2014) and drought-intolerant species (Vann et al., 2005). The second group, the anisohydric species *Betula* (Ishii et al., 2013), *Castanea* (Fardusi et al., 2016; Gomes-Laranjo et al., 2012) and *Fagus* (Hartl-Meier et al., 2015; Pretzsch et al., 2013; Zang et al., 2014) are classified to follow water-spending strategies (Fardusi et al., 2016). During drought, these species maintain negative water potentials and continue transpiration and biomass production (Woodruff et al., 2016). For the year 2003, a relatively high resistance ( $R_s = 0.66$ – $0.78$ ) and low recovery ( $R_c = 1.12$ – $1.30$ ) could therefore be attributed to sustained stomatal conductance for these three species (Fig. 7a). Additionally, the low growth depressions ( $R_s = 0.78$  and  $0.86$ ) and low recovery ( $R_c = 1.30$  and  $1.29$ ) of *Castanea* and *Fagus* in 2006 as well as in 2010/11 for *Castanea* ( $R_s = 0.75$ ,  $R_c = 1.36$ ) might be caused by spending strategy. In particular, the mesophilic South European *Castanea sativa* (Gomes-Laranjo et al., 2012) seem to profit from anisohydric character suggesting high adaptive potential (high  $R_s$  for individual stress events). Nevertheless, growth of *Castanea* was found to be limited by water availability in winter, or continuous heat during spring and summer,

leading to over-transpiration and synergic damages (e.g. blight and ink disease; Conedera et al., 2010; Waldboth and Oberhuber, 2009). The Japanese *Betula maximowicziana* is largely characterized as a drought-intolerant species (Koike and Sakagami, 1985; Niinemets and Valladares, 2006; Ranney et al., 1991). However, among the genus *Betula*, *B. maximowicziana* is considered to be one of the more resistant birches (Leder and Tennhoff, 2014; Shaw et al., 2014). In this study, *Betula* trees benefited from high growth stability during long-lasting summer drought in 2003 (highest  $R_s = 0.78$ ) related to anisohydric strategy.

We conclude that both, long-term adaptations due to origin and physiological mechanisms, may cause species-specific drought response behaviour. For *Cryptomeria* and *Picea*, the isohydric behaviour and less favourable site conditions may explain the low drought resistance. However, both species benefit from high responsiveness after disturbance at our study site. As long as changes in climatic conditions do not result in long-lasting water shortages, both species may actually profit from their strong ability to recover. Nevertheless, repeated successive drought events may have an increasingly negative impact on their productivity in the future (cf. 2010 and 2011). Accumulated growth declines may not be compensated for, and ongoing stress can lead to problems related to deficits in defensive mechanisms (e.g. bark beetles; Anderegg et al., 2015). This is likely to be of special importance on dry sites. In contrast, the low sensitivity of species such as *Castanea*, *Thuja* and *Tsuga* seems to promote high plasticity to more frequent and variable drought periods (short- and long-term drought). *Thuja* and *Tsuga* may benefit from wide ecological amplitudes while the growth of *Castanea* is promoted by water-spending, anisohydric physiology. As a result, cultivation with such species may reduce silvicultural risks to stress events of different magnitudes (Bolte et al., 2009). *Betula* and *Fagus* seem to profit from high growth stability during the major drought in 2003 or short-term drought periods in 2006, respectively. In comparison to *Betula*, *Fagus* trees are more adaptable to changing aridity as resistance, recovery and resilience across different stress events is higher. For both species, moderate to high drought tolerances may be related to an anisohydric strategy and, in the case of *Fagus*, to favourable site conditions. *Acer* and *Metasequoia* are characterized by greater sensitivity to and higher recovery from short-term summer drought (2006) that may be associated with isohydric behavior in early stages of water shortage. However, the ability to recover from long-lasting rainfall deficits (2003 and 2010/11) is comparatively low for these species. As summarized by rather intermediate growth stability across the analysed drought events, *Metasequoia* can be classified as moderate drought-tolerant. However, the general low resistance and resilience and rather moderate recovery lead to characterize *Acer* as the least drought-tolerant species at Burgholz site.

#### 4.3. Growth variations along the stem

Significant correlations between growth chronologies of different height sections and of various growth variables (BAI and VI) for the majority of species indicate that increment indices at breast height ( $RI_{1.3}$ ,  $BAI_{1.3}$ ) are useful estimators for annual volume production. This finding corresponds to results of other studies (e.g. LeBlanc, 1990; Metsaranta and Bhatti, 2016; Rais et al., 2014). Nevertheless, with strong tapering and consequently increasing diameter-height ratios, the explanatory power of  $BAI_{1.3}$  values decreased with increasing longitudinal distance to breast height (e.g. *Thuja* and *Tsuga*; Fig. 5). For the majority of species, mean sensitivity and drought response were inconsistent along the stem. We found that inter-annual variation at breast height ( $BAI_{1.3}$ ) systematically overestimated  $ms$  of the above-ground stem production ( $VI_{TS}$ ) for six out of the nine tree species (by 19.6% on average across these species; Table 1). This finding is in line with other studies that have observed comparable breast height-to-whole stem discrepancies in  $ms$  for lodgepole pine, silver fir and European beech (Chhin et al., 2010; Latte et al., 2016; van der Maaten-

Theunissen and Bouriaud, 2012). The proportionality of  $ms$  between  $BAI_{1.3}$  and  $VI_{TS}$  is partly evident in drought response indices, suggesting an overall greater response to drought (stronger decline during and stronger recovery after drought) of  $BAI_{1.3}$  when compared with  $VI_{TS}$  for the event year 2003 (Fig. 8a).

Within main trunks of up to 13.3 m tree height, we found little (*Picea*, *Cryptomeria*) to strong (*Betula*, *Thuja*) variation in  $ms$  and drought index values (Figs. 6 and 8b). The lower  $ms$  and less pronounced drought response with increasing stem height in most species may result from disproportionately higher carbon (C) allocation at the treetop and time lags of C transport from regions close to the organs of photosynthesis (foliage) to lower stem sections (Gower et al., 1995; Sevanto et al., 2003). During drought occurrence, reduced C assimilates are allocated primarily to upper stem parts (Woodruff and Meinzer, 2011). As a consequence, the basipetal (top-down) transport of carbohydrates is reduced, resulting in relatively low growth rates at lower bole sections, which in turn may lead to stronger growth reductions during drought stress (Chhin et al., 2010; Larson, 1963; Sohn et al., 2012).

However, several authors have proposed the theory of hydraulic and gravitational limitations inhibiting water availability at the tops of tall trees (e.g. Ishii et al., 2008; Koch et al., 2004; McDowell et al., 2002). Therefore, increasing climate sensitivity is assumed to increase at high stem positions (Kerhoulas and Kane, 2012). Supporting this, Bouriaud et al. (2005) and Latte et al. (2016) reported slight decreases in  $ms$  along the main bole, which gradually changed resulting in highest sensitivity at the topmost section within the crown. In conclusion, both mechanisms (carbon allocation and hydraulic limitations) are expected to interact, but their impacts on tree growth are not universal (Ryan et al., 2006; Ryan and Yoder, 1997). In fact, the drought responses of most of our study trees seem to be largely controlled by basipetal carbon allocation.

#### 4.4. Limitations and methodical considerations

Similar to further studies, combining dendroecological methods and stem analyses, this approach refers to a small spatial scale (one study site; e.g. Latte et al., 2016; Sohn et al., 2012). Hence, implications regarding species-specific responses are limited to regions with comparable site (including climatic) conditions and does not necessarily reflect general species behaviour. However, this fact should not preponderate since this study is, so far, the first analysis with joint data of these poorly considered rare tree species for this geographical region in Europe.

The small sample size (6–10 trees) affects the statistical evidence concerning the climatic signal strength of the growth chronologies. In this study, we used the expressed population signal ( $eps$ , with a threshold level of  $eps = 0.85$ ) that has been (mistakenly) widely used to verify climatic evidences of chronologies (Buras 2017). Indeed, the  $eps$  is a helpful means for evaluation of the representation of the population signal, and will likely but not necessarily reflect the power of reconstructed climatic signal (Buras 2017). Hence, disturbances by the noise of other factors (e.g. endogen factors or human activity) cannot be excluded with statistical certainty (Bhuyan et al., 2017).

Furthermore, some controversy exists with respect to the ambiguous interpretation of the mean sensitivity ( $ms$ ; e.g. Biondi and Qeadan, 2008; Bunn et al., 2013). Bunn et al. (2013) indicated that the varying impact of growth-limiting factors cannot be deduced from  $ms$  while the dependency of  $ms$  upon the variance of this factor is neglected. However, findings from Wright et al. (2016) pointed out a strong similarity between the regression results (tree growth and environmental influences) using  $ms$  and the recommended substitute statistics, standard deviation (Bunn et al., 2013) and Gini coefficient (Biondi and Qeadan, 2008). Accordingly, we found strong relationships between  $ms$  and the suggested measures standard deviation and Gini coefficient ( $R = 0.84$ – $0.95$  and  $R = 0.83$ – $0.95$ , respectively, for individual species



series), with almost identical results concerning species-specific and stem-height related differences (data not shown; cf. Table 1). We strictly emphasize that the usage of the measure *ms* in our study focus on the general description of inter-annual growth variation to highlight differences in growth dynamics among and within species. The assessment of dependencies of tree growth upon selected climate predictors (for different time scales) is planned for subsequent analyses.

## 5. Conclusions

Our study emphasises that drought tolerance and mean sensitivity were not uniform among tree species and drought events. Furthermore, growth responses decreased species-specifically with stem height, indicating a bias when using breast-height measurements to predict whole-tree volume response. We conclude that the tree species studied here follow individual strategies to mitigate drought stress. In addition, depending on the onset and duration of drought events, the species differ in their ability to withstand growth decline and to maintain vitality. Our study suggests that some alien species may exceed the tolerance levels of native species. More precisely, western hemlock (*Tsuga heterophylla*), sweet chestnut (*Castanea sativa*) and western red cedar (*Thuja plicata*) were most tolerant to variable drought stress; whereas Norway spruce (*Picea abies*), Japanese red-cedar (*Cryptomeria japonica*) and red maple (*Acer rubrum*) were the most sensitive tree species. The variation in growth response with tree heights indicates under- or overestimation of drought sensitivity if an investigation takes only one tree height section into account. Our study emphasizes the need for multi-species comparisons at equivalent site conditions and the consideration of whole stem increment attributes in order to provide reliable indices for an appropriate classification of the climate adaptability of tree species.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agrformet.2018.03.008>.

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